

# SPORES OF THE HETEROPHYLLOUS *SELAGINELLAE* OF MEXICO AND CENTRAL AMERICA<sup>1</sup>

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## ABSTRACT

Megaspores and microspores of forty-six species and a presumed hybrid of heterophyllous *Selaginellae* from Mexico and Central America are described. Characters of the spores are correlated with three major groupings—the articulate group, the non-articulate group, and, within the latter, the group containing those species which curl into a ball when dried. A key based on spore and sporangial characters is included.

The genus *Selaginella* has attracted much attention from morphologists because of its heterospory, its stelar anatomy, and its controversial organ, the rhizophore. The genus is nearly worldwide in distribution, although most of the species are tropical. *Selaginella* is generally divided into two subgenera: homophyllous species are placed in subgenus *Selaginella*; heterophyllous species (having two dorsal rows of smaller leaves and two lateral rows of larger leaves) are placed in subgenus *Stachygynandrum*. The latter has been further divided on the basis of habit, articulation of the stems, arrangement of the leaves, and geographical distribution (Greville & Hooker, 1831; Spring, 1850; Braun, 1860; Baker, 1883; Hieronymus, 1902; Alston, 1955). Stem articulation in *Selaginella* is presumed rather than real. At each node (site of stem ramification) in the “articulate” species there is a narrow constriction or discoloration of the main stem that is suggestive of an abscission layer.

Alston (1955) prepared a key to the heterophyllous species of *Selaginella* of North America south to Panama. He grouped the species largely according to the characters used in previous classifications but occasionally made use of spore characteristics to separate difficult groups. The spore characters he used are color of both megaspores and microspores and ornamentation of the microspores. Tryon (1949) described the spores of the American species of *Selaginella* which occur north of Mexico. These are largely homophyllous species.

Unpublished work by Mickel shows that the heterophyllous *Selaginellae*, which are mostly tropical, are more diverse in spore morphology than the homophyllous species. The present study describes the spores of the heterophyllous species of Mexico and Central America, especially with regard to color, size, and ornamentation. This information will be correlated with previous taxonomic groupings. This study is preliminary in nature and will undoubtedly be corrected and amplified by further investigation of this group.

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<sup>1</sup> Based on a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science, Iowa State University, Ames, Iowa. I thank Dr. John T. Mickel for pointing out the problem and for his assistance in the course of the study.

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TABLE 1. Specimens on which the descriptions of spores are based.

<i>Selaginella anceps</i> .	<i>Selaginella martensii</i> .
COSTA RICA: Mickel 2696 (NY).	MEXICO: Mickel 948 (ISC).
<i>Selaginella arthritica</i> .	<i>Selaginella microdendron</i> .
COSTA RICA: Mickel 3334 (NY).	MEXICO: Rzedowski 10670 (ISC).
<i>Selaginella articulata</i> .	BRITISH HONDURAS: Schipp 99 (NY).
PANAMA: Lewis, MacBryde, Oliver & Ridgway 1777 (MO).	<i>Selaginella minima</i> .
<i>Selaginella bombycina</i> .	PANAMA: Johnston 878 (US).
PANAMA: Allen 2225 (MO).	<i>Selaginella mollis</i> .
<i>Selaginella cladorrhizans</i> .	COSTA RICA: Molina, Williams, Burger & Wallenta 17144 (NY).
MEXICO: Mexia 8725 (MO, NY).	<i>Selaginella novae-hollandiae</i> .
<i>Selaginella delicatissima</i> .	PANAMA: Burch, Oliver & Solis 1088 (MO, NY).
MEXICO: Mickel 1114 (ISC).	<i>Selaginella novoleonensis</i> .
<i>Selaginella estrellensis</i> .	MEXICO: King 4559 (ISC, NY).
COSTA RICA: Stork 1755 (MO).	<i>Selaginella oaxacana</i> .
GUATEMALA: Cooper 6062 (NY).	MEXICO: Mickel 947 (ISC).
<i>Selaginella eurynota</i> .	<i>Selaginella ovifolia</i> .
COSTA RICA: Brenes 5783 (NY); Skutch 2216 (MO).	BRITISH HONDURAS: Schipp 924 (US).
<i>Selaginella exaltata</i> .	<i>Selaginella pallescens</i> .
COSTA RICA: Mickel 1988 (NY).	MEXICO: Mickel 1169 (ISC).
<i>Selaginella flagellata</i> .	<i>Selaginella porphyrospora</i> .
COLOMBIA: Smith 2245 (ISC).	MEXICO: Mickel 1560 (NY).
<i>Selaginella galeottii</i> .	<i>Selaginella pulcherrima</i> .
MEXICO: Mickel 894 (ISC).	MEXICO: Conzatti 807 (US).
<i>Selaginella guatemalensis</i> .	<i>Selaginella reflexa</i> .
HONDURAS: Yuncker, Dawson & Youse 5840 (MO).	MEXICO: Pringle 10326 (NY).
GUATEMALA: Maxon & Hay 3297 (NY).	<i>Selaginella revoluta</i> .
<i>Selaginella haematodes</i> .	COLOMBIA: Hermann 10975 (US).
PANAMA: Burch, Oliver & Solis 1079 (MO).	VENEZUELA: Williams 11379 (US).
<i>Selaginella hoffmannii</i> .	<i>Selaginella schaffneri</i> .
MEXICO: Hellwig 467 (ISC).	MEXICO: Pringle 15630 (US); Schaffner 8 (NY).
<i>Selaginella horizontalis</i> .	<i>Selaginella schiedeana</i> .
PANAMA: Allen 2013 (NY); Johnston 1142 (MO).	MEXICO: Pringle 5415 (ISC).
<i>Selaginella huehuetenangensis</i> .	<i>Selaginella schizobasis</i> .
PANAMA: Smith & Smith 3305 (ISC).	MEXICO: Ghiesbreght 605 (NY).
GUATEMALA: Standley 24173 (NY).	<i>Selaginella sertata</i> .
<i>Selaginella idiospora</i> .	MEXICO: Rzedowski 14912 (NY).
COSTA RICA: Mickel 3276 (NY).	<i>Selaginella silvestris</i> .
<i>Selaginella illecebrosa</i> .	HONDURAS: Yuncker, Koepper & Wagner 8490 (MO).
GUATEMALA: Steyermark 41579 (US).	COSTA RICA: Kuntze 2014 (NY).
<i>Selaginella intacta</i> .	<i>Selaginella stenophylla</i> .
COSTA RICA: Mickel 2645 (NY).	MEXICO: Mickel 625 (ISC).
<i>Selaginella kunzeana</i> .	<i>Selaginella tarapotensis</i> .
COSTA RICA: Jimenez 1706 (NY); Skutch 3106 (MO).	MEXICO: Mickel 956 (ISC); Mickel 946 (NY).
<i>Selaginella lepidophylla</i> .	<i>Selaginella umbrosa</i> .
MEXICO: Knobloch 1919 (ISC); Pringle 5417 (ISC).	BRITISH HONDURAS: Wilson 217 (NY).
<i>Selaginella lychnuchus</i> .	<i>Selaginella unknown species 1</i> .
MEXICO: Palmer 265 (MO).	MEXICO: Mickel 1086 (NY).
COSTA RICA: Mickel 2310 (ISC).	<i>Selaginella unknown species 2</i> .
<i>Selaginella marginata</i> .	MEXICO: Mickel 1579 (NY).
MEXICO: Pennell 20187 (US).	Presumed hybrid.
	MEXICO: Rzedowski & McVaugh 5 (NY).



## MATERIALS AND METHODS

This study is based on materials obtained from the herbaria of Iowa State University, the New York Botanical Garden, the United States National Museum, and the Missouri Botanical Garden. The specimens on which the descriptions are based are listed in Table 1. The author expresses appreciation to the curators of these herbaria for making specimens available.

Basically the species in this study are those found in Alston's key (1955). Excluded are a few species which are limited to North America north of Mexico. Material of some species treated by Alston was not available. Also missing are species specimens of which lacked cones, had shed their spores, or had immature spores. Despite these deficiencies 46 species and a presumed hybrid from Mexico were examined.

In this preliminary study, spores from one specimen, if both megaspores and microspores were present, were used to avoid possible confusion should the specimen later be found to be misidentified. Spores were removed from the strobili (from naturally opened sporangia in most cases) and placed on white paper. They were observed at 10 $\times$  and color was determined according to Ridgway (1912). In the descriptions the color from Ridgway is followed by a vernacular equivalent, if the color is not obvious from the formal name. The spores were then directly mounted and cleared in Hoyer's medium (Anderson, 1954) and dried on a heating tray at 56° C.

Spore measurements were made from the preparations using a Leitz Labolux microscope fitted with an ocular micrometer. Different magnifications were used for the various sizes of spores. An attempt was made to measure 20 free microspores from each species. The number of megaspores measured depended on the number readily available. In the spore descriptions the three measurements are the minimum, the average (*italicized*), and the maximum spore sizes respectively. The diameter of the megaspores, excluding the muri, was measured; the spines and other projections were not included in the measurements of the microspores. The drawings were done with the aid of a Zeiss drawing apparatus.

## SPORE DESCRIPTIONS

The spores of the heterophyllous *Selaginellae* are tetrahedral with a triradiate scar on the proximal face. The megaspores are generally marked by undulating, anastomosing muri or ridges which may form flanges at the equator and/or along the scar. High muri range from 100–150 $\mu$ ; low muri are from 15–50 $\mu$  in height. There is generally less ornamentation on the proximal face than on the distal face. The microspores generally have papillae or spines, rarely ridges. Terms for the wall layers, such as exospore and perispore, have been purposely avoided, since the origin of the wall layers is a matter of controversy. The outer part of the high muri is of a granular, more translucent material than that of the base. In many species the megaspore wall has very fine markings that are seen both in the areoles and beneath the muri suggesting that the muri are of a different nature.

The sporangia of *Selaginella* are generally arranged in four vertical rows in the strobili. Horner and Arnott (1963) have shown the taxonomic significance of the patterns of sporangial distribution. Therefore, the patterns of distribution are noted. The patterns include: one basal megasporangium per strobilus; two longitudinal rows of megasporangia and two longitudinal rows of microsporangia per strobilus; wholly megasporangiate or microsporangiate strobili; and various mixed patterns.

In order to facilitate comparison of taxonomic groupings and previous descriptive works, the sequence of presentation is that of Alston's key (1955). The spores are described with reference to color, size, and ornamentation as in Tryon (1949), and notes on sporangial distribution and other pertinent features are



added when possible. A provisional key to the species considered in this study is provided.

#### NON-ARTICULATE SPECIES

##### *Selaginella novoleonensis* Hieron.

*Megaspores.* Cadmium Yellow (gold); 127–326–382 $\mu$  in diameter, 10 spores measured; muri quite high on both faces with extensions forming flanges and high curved peaks at some places; spores from each sporangium highly variable in size; strobili with two longitudinal rows of each type of sporangium (Fig. 13–14).

*Microspores.* Bittersweet Orange (highly variable); tetrad size 69–79–91 $\mu$  in diameter, 10 tetrads measured, individual spore outline as seen through outer wall about 25 $\mu$  in diameter; common wall around the spores undulate and fluted at one end, nearly smooth at the other (Fig. 52).

##### *Selaginella lepidophylla* (Hook. & Grev.) Spring.

*Megaspores.* Lemon Chrome (yellow); 245–321–413 $\mu$  in diameter, 5 spores measured; with high irregular ridges on both proximal and distal faces, often elongate into spines. Strobili mixed; most of the sporangia microsporangiate.

*Microspores.* Mikado Orange; tetrad 76–79–87 $\mu$  in diameter, 4 tetrads measured, individual spore outlines 32–39 $\mu$  in diameter. Spores shed in tetrads surrounded by a common, heavily undulate wall.

##### *Selaginella pallescens* (Presl) Spring.

*Megaspores.* Clay Color; 387–418–448 $\mu$  in diameter, 4 spores measured; ridges thin and vein-like; megasporangia in the lower part of the strobili (Fig. 7–8).

*Microspores.* Scarlet; 21–22–24 $\mu$  in diameter, 20 spores measured; papillae short, capitate.

##### *Selaginella microdendron* Baker.

*Megaspores.* Pale Ochraceous Buff (very pale orange); 306–352–392 $\mu$  in diameter, 6 spores measured; with low, broad ridges, even on proximal face; strobili loosely constructed of a few sporophylls, no constant pattern of sporangial arrangement.

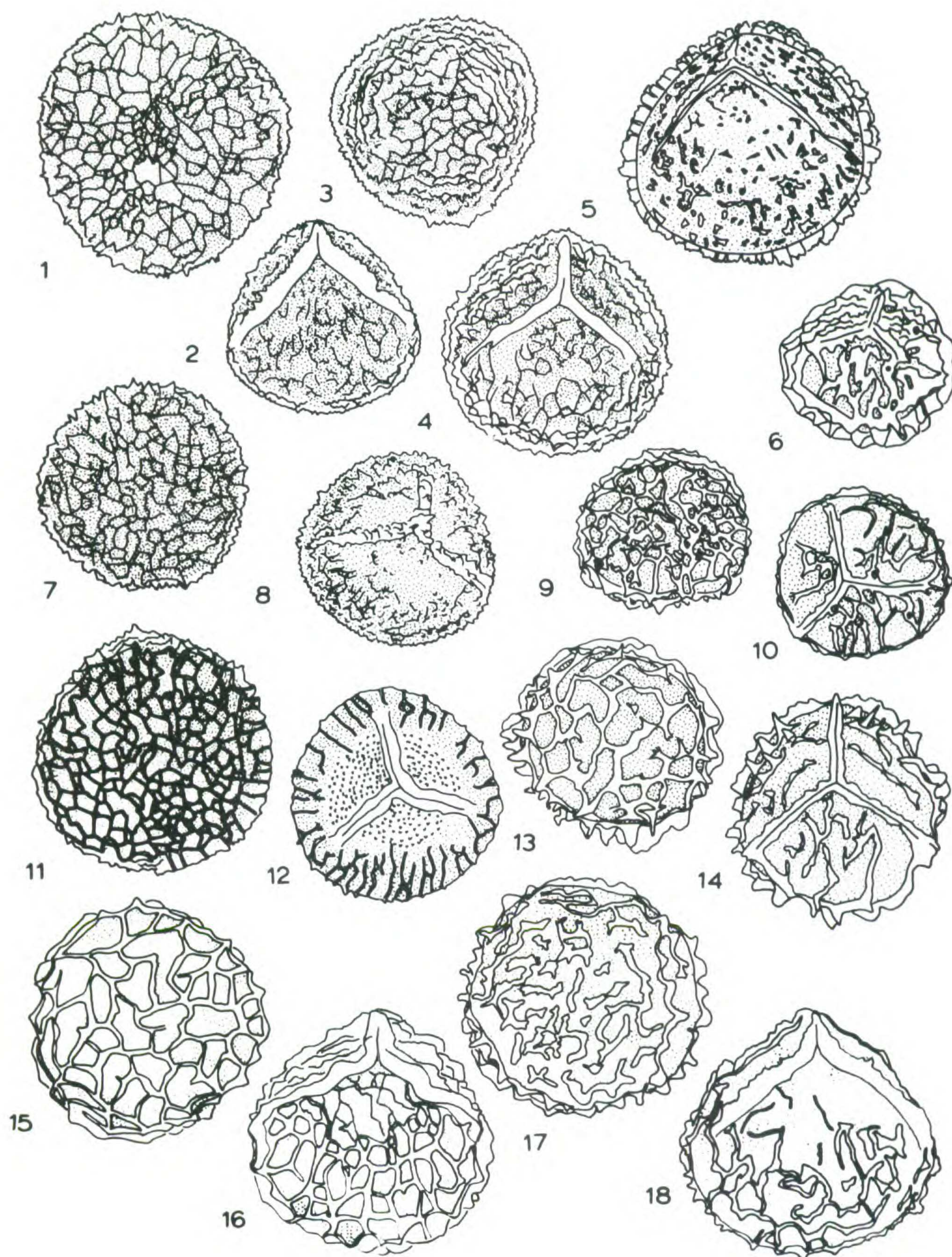
*Microspores.* Orange; heavy capitate papillae.

##### *Selaginella umbrosa* Lemaire ex Hieron.

*Megaspores.* White; 209–224–240 $\mu$  in diameter, 10 spores measured; with low ridges; spores extremely thin-walled with all the larger ones breaking, the measurements are therefore too low; megasporangia and microsporangia in two longitudinal rows.

*Microspores.* Bittersweet Orange; 20–22–24 $\mu$  in diameter, 20 spores measured; with sparse, short papillae (Fig. 32–33).







*Selaginella haematodes* (Kunze) Spring.

*Megaspores.* Maize Yellow (off-white); 204–235–296 $\mu$  in diameter, 6 spores measured; ridges low to medium in height; strobili with two rows of megasporangia and two rows of microsporangia.

*Microspores.* Light Salmon-Orange; 21–23–29 $\mu$  in diameter, 20 spores measured; with sparse, rounded to capitate papillae.

*Selaginella hoffmannii* Hieron.

*Megaspores.* White; 240–275–316 $\mu$  in diameter, 7 spores measured; with low ridges; strobili possibly with two rows of microsporangia together and two rows of megasporangia opposite them.

*Microspores.* Grenadine Red (bright orange); 21–28–31 $\mu$  in diameter, 20 spores measured; ridges narrow with occasional blunt spine-like projections.

*Selaginella bombycina* Spring.

*Megaspores.* White; 306–316–326 $\mu$  in diameter, 5 spores measured; with low ridges; strobili with two rows of each type of sporangium, some exceptions noted.

*Microspores.* Bittersweet Orange; 29–36–40 $\mu$  in diameter, 20 spores measured; with low capitate papillae.

*Selaginella anceps* Presl.

*Megaspores.* White; 235–245–260 $\mu$  in diameter, 7 spores measured; with low narrow ridges; spores break very easily; very few megasporangia per strobilus.

*Microspores.* Salmon-Orange; 22–24–26 $\mu$  in diameter, 20 spores measured; papillae small; many spores of irregular shape.

*Selaginella oaxacana* Spring.

*Megaspores.* Cream Color; 362–382–413 $\mu$  in diameter, 4 spores measured; distal face with low narrow ridges, proximal face with granular emergences to papillae (Fig. 11–12).—There is some tendency toward inequality of spore size in any one sporangium. The megasporangia make up the basal half of the strobilus.

*Microspores.* Bittersweet Orange; 21–23–26 $\mu$  in diameter, 14 spores measured; with few broad, short papillae; most of the spores in tetrads.

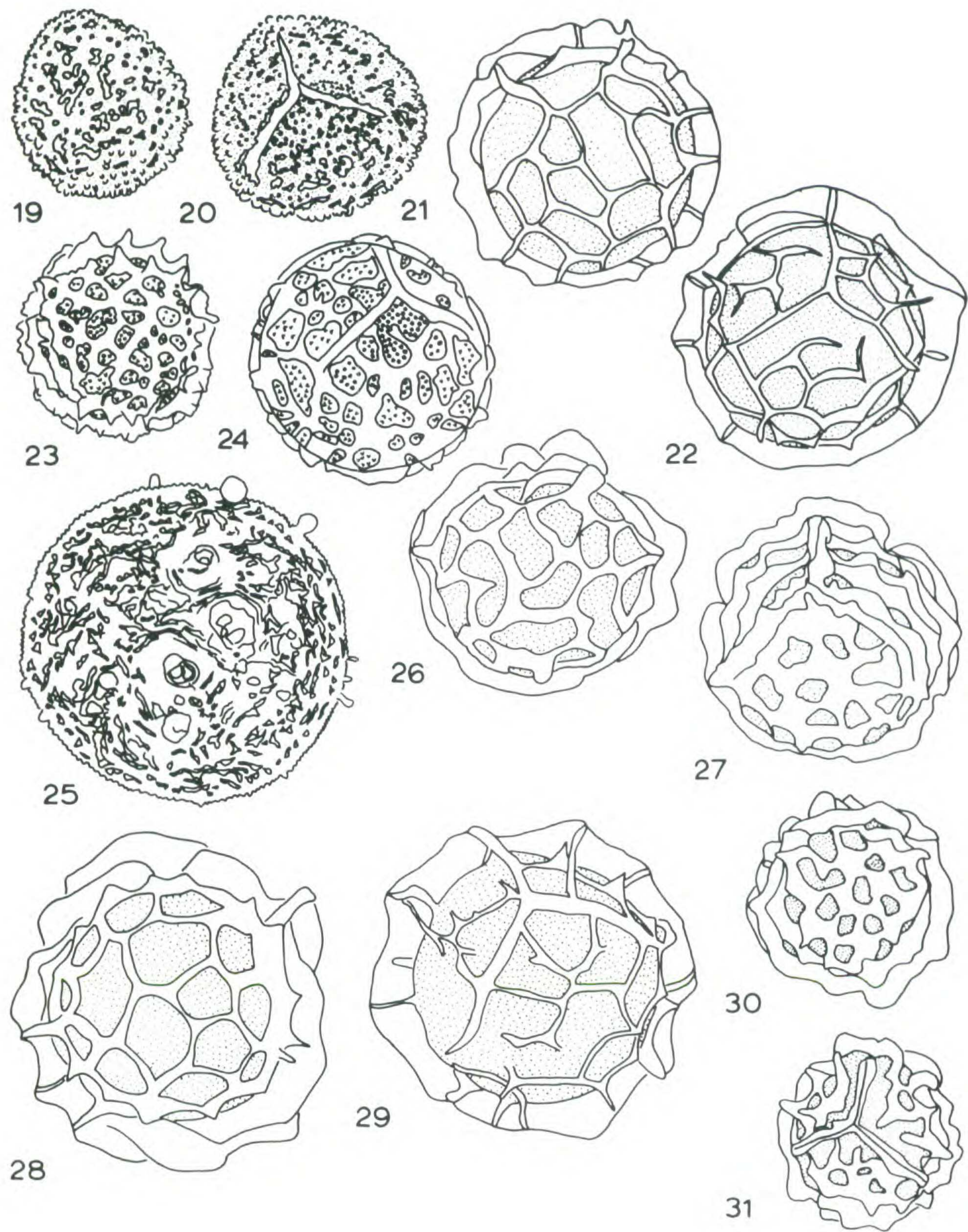
*Selaginella pulcherrima* Liebm. & Fourn.

*Megaspores.* Pale Orange-Yellow (beige); 300–338–398 $\mu$  in diameter, 3 spores measured; with low, narrow ridges, minute papillae between and on ridges,



FIGURES 1–18.—Megaspores of *Selaginella*. — 1–2. *S. guatemalensis*,  $\times 120$ .—1. Distal face.—2. Proximal face. — 3–4. *S. idiospora*,  $\times 120$ .—3. Distal face.—4. Proximal face. — 5. *S. schaffneri*, proximal face,  $\times 120$ . — 6. *S. porphyrospora*, proximal face,  $\times 120$ . — 7–8. *S. pallescens*,  $\times 120$ .—7. Distal face.—8. Proximal face. — 9–10. *S. stenophylla*,  $\times 120$ . 9. Distal face.—10. Proximal face. — 11–12. *S. oaxacana*,  $\times 120$ .—11. Distal face.—12. Proximal face. — 13–14. *S. novoleonensis*,  $\times 120$ .—13. Distal face.—14. Proximal face. — 15–16. *S. mollis*,  $\times 125$ .—15. Distal face.—16. Proximal face. — 17–18. *S. tarapotensis*,  $\times 125$ .—17. Distal face.—18. Proximal face.







and on proximal face; few microsporangia in each strobilus.

*Microspores.* Bittersweet Orange;  $26-30-36\mu$  in diameter, 20 spores measured; sparingly papillose.

*Selaginella illecebrosa* Alston.

*Megaspores.* Pale Yellow-Orange (beige);  $245-292-321\mu$  in diameter, 10 spores measured; ridges of medium height.—The bottom half of the strobilus appears to be megasporangiate with very few microsporangia in the upper half.

*Microspores.* Xanthine Orange (orange-brown);  $19-20-23\mu$  in diameter, 20 spores measured; with large rounded or capitate papillae; some spores remaining in tetrads.

*Selaginella schaffneri* Hieron.

*Megaspores.* Grenadine Pink (orange) with white ridges;  $367-402\mu$  in diameter, 2 spores measured; ridges low to medium in height, uneven, sparsely anastomosing (Fig. 5).—Many spores broke in preparation. There are a few basal megasporangia per strobilus, and the rest of the strobilus contains a few microsporangia very close to the lower part or distant from it.

*Microspores.* Bittersweet Pink, Light Salmon Orange, Bittersweet Orange, and Salmon Orange;  $47-56-63\mu$  in diameter, 20 spores measured; heavy, broad ridges cover most of the distal face, leaving a few cavities; spores often in tetrads (Fig. 55–56).

*Selaginella delicatissima* Linden.

*Megaspores.* Empire Yellow (dark yellow);  $443-473-494\mu$  in diameter, 3 spores measured; with low papillae merging to form short, irregular ridges; unequally-sized spores in each sporangium; megasporangia generally located in the lower half of the strobilus (Fig. 19–20).

*Microspores.* Orange Chrome;  $40-47-55\mu$  in diameter, 20 spores measured; ornamentation highly variable, ranging from densely papillose to irregularly ridged, on both faces (Fig. 57–59).

*Selaginella tarapotensis* Baker.

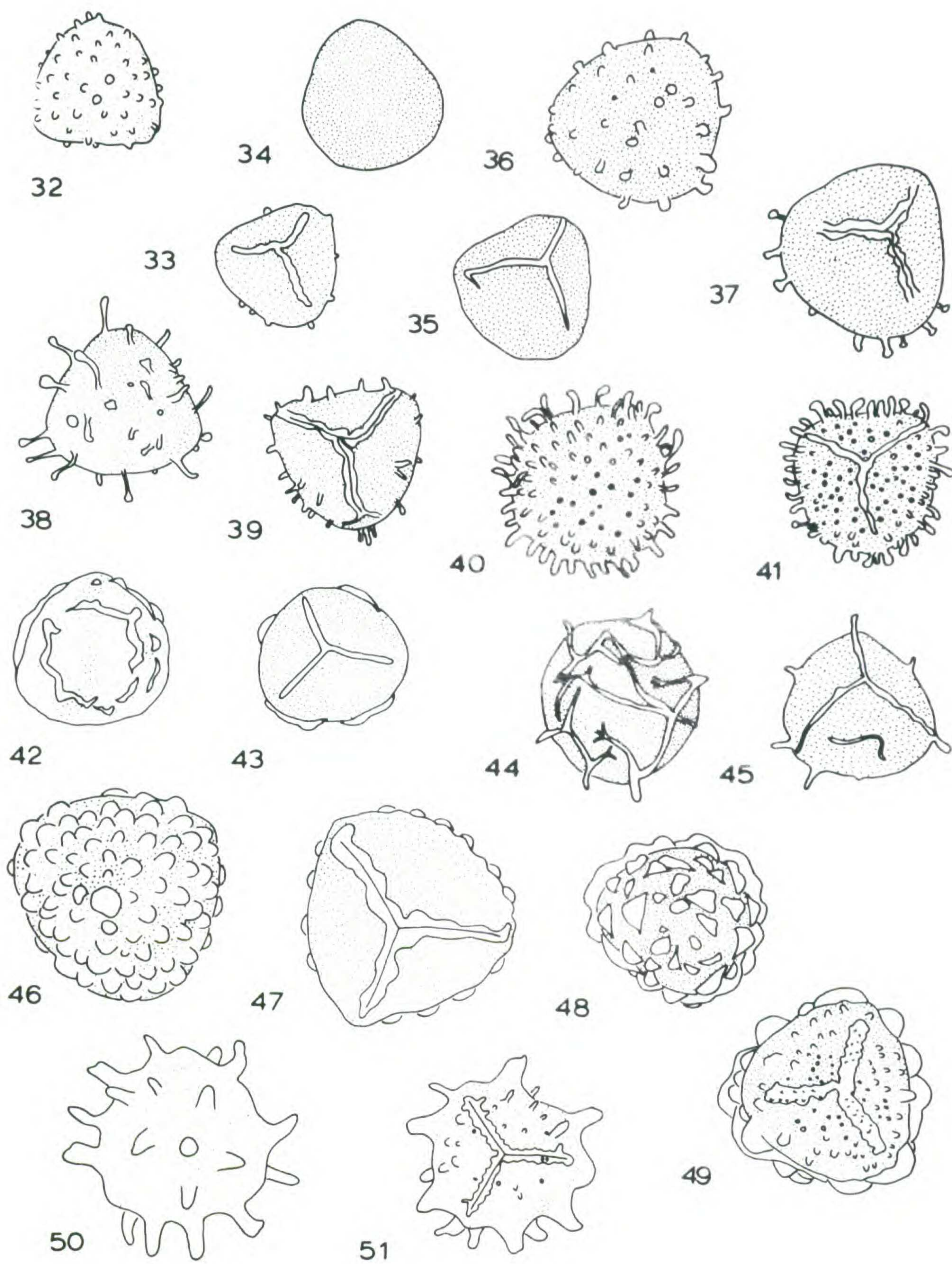
*Megaspores.* Cream Color;  $255-275-291\mu$  in diameter, 6 spores measured; with very low ridges; many broken open in preparation; megasporangia basal (Fig. 17–18).

*Microspores.* Bittersweet Orange;  $25-28-29\mu$  in diameter, 20 spores measured; papillae slender to capitate (Fig. 36–37).



FIGURES 19–31.—Megaspores of *Selaginella*. — 19–20. *S. delicatissima*,  $\times 60$ .—19. Distal face.—20. Proximal face. — 21–22. *S. sertata*,  $\times 60$ .—21. Distal face.—22. Proximal face. — 23–24. *S. intacta*,  $\times 60$ .—23. Distal face.—24. Proximal face. — 25. Presumed hybrid,  $\times 60$ . — 26–27. *S. arthritica*,  $\times 60$ .—26. Distal face.—27. Proximal face. — 28–29. *S. exaltata*,  $\times 30$ .—28. Distal face.—29. Proximal face. — 30–31. *S. articulata*,  $\times 30$ .—30. Distal face.—31. Proximal face.







*Selaginella ovifolia* Baker.

*Megaspores.* Cream Buff (beige); 219–224–240 $\mu$  in diameter, 4 spores measured; ridges low.

*Microspores.* Flame Scarlet; 30–36–39 $\mu$  in diameter, 20 spores measured; with short, broad papillae (Fig. 46–47).

*Selaginella reflexa* Underw.

*Megaspores.* Picric Yellow; 321–336–367 $\mu$  in diameter, 5 spores measured; with broad muri of medium height extending to triradiate crest; tendency toward unequally-sized spores; very few microsporangia.

*Microspores.* Bittersweet Orange; 29–32–36 $\mu$  in diameter, 20 spores measured; ridge-like papillae highly irregular in size and shape, apparently at least partially abortive (Fig. 48–49).

*Selaginella guatemalensis* Baker.

*Megaspores.* Light Buff (pale orange); 342–377–458 $\mu$  in diameter, 4 spores measured; with low ridges; most spores broken in preparation; megasporangia basal (Fig. 1–2).

*Microspores.* Pale Orange-Yellow (beige); 24–28–31 $\mu$  in diameter, 20 spores measured; high narrow ridges (Fig. 44–45).

*Selaginella huehuetenangensis* Hieron.

*Megaspores.* White; 316–372–407 $\mu$  in diameter, 8 spores measured; wall marked by a reticulate pattern, but ridges lacking; megasporangia basal.

*Microspores.* Bittersweet Orange; 23–26–31 $\mu$  in diameter, 20 spores measured; with narrow ridges and elongate spine-like projections.

*Selaginella idiospora* Alston.

*Megaspores.* Light Cinnamon Drab (brown-gray); 321–362–392 $\mu$  in diameter, 10 spores measured; ridges low with very fine networks or papillae within the areoles; megasporangia few and basal (Fig. 3–4).

*Microspores.* Salmon-Buff (pale orange); 23–24–26 $\mu$  in diameter, 20 spores measured; with low, broad papillae with hints of narrow, interconnecting ridges (Fig. 42–43).—Many spores are in tetrads, as Alston (1955) mentions in his key.

*Selaginella revoluta* Baker.

*Megaspores.* Cream Color; 275–281 $\mu$  in diameter, 2 spores measured; with narrow, uncrowded muri of medium height; most spores broken in preparation.—



FIGURES 32–51.—Microspores of *Selaginella*. — 32–33. *S. umbrosa*,  $\times 600$ .—32. Distal face.—33. Proximal face. — 34–35. *S. revoluta*,  $\times 600$ .—34. Distal face.—35. Proximal face. — 36–37. *S. tarapotensis*,  $\times 600$ .—36. Distal face.—37. Proximal face. — 38–39. *S. flagellata*,  $\times 600$ .—38. Distal face.—39. Proximal face. — 40–41. *S. exaltata*,  $\times 600$ .—40. Distal face.—41. Proximal face. — 42–43. *S. idiospora*,  $\times 600$ .—42. Distal face.—43. Proximal face. — 44–45. *S. guatemalensis*,  $\times 600$ .—44. Distal face.—45. Proximal face. — 46–47. *S. ovifolia*,  $\times 600$ .—46. Distal face.—47. Proximal face. — 48–49. *S. reflexa*,  $\times 600$ .—48. Distal face.—49. Proximal face. — 50–51. *S. marginata*,  $\times 600$ .—50. Distal face.—51. Proximal face.



The strobili are almost totally megasporangiate with only one microsporangium at the top.

*Microspores.* Flame Scarlet; 22–25–28 $\mu$  in diameter, 20 spores measured; no markings (Fig. 34–35).—Perhaps the spores were immature, although they were all separate.

*Selaginella schiedeana* A. Braun.

*Megaspores.* Pinard Yellow; 331–402–469 $\mu$  in diameter, 10 spores measured; with narrow ridges of medium height; three small spores and one large one in each sporangium.—There are a few basal megasporangia per strobilus.

*Microspores.* Grenadine Red (bright orange); 29–42–56 $\mu$  in diameter, 20 spores measured; with short, broad papillae, even on the proximal face; many irregular in size and shape (Fig. 53–54).

*Selaginella cladorrhizans* A. Braun.

*Megaspores.* Yellow; 202–210–218 $\mu$  in diameter, 4 spores measured; ridges often peaked; strobili with two longitudinal rows of each type of sporangium.

*Microspores.* Flame Scarlet, 25–28–31 $\mu$  in diameter, 20 spores measured; with stoutly capitate projections.

*Selaginella lychnuchus* Spring ex Klotzsch.

*Megaspores.* Light Buff (pale orange); 296–311–336 $\mu$  in diameter, 9 spores measured; with ridges low, sparsely anastomosing, with frequent papillae on the ridges; two rows of each type of sporangium.

*Microspores.* Grenadine (orange); 24–28–31 $\mu$  in diameter, 20 spores measured; papillae low and broad to capitate; many spores in tetrads.

*Selaginella stenophylla* A. Braun.

*Megaspores.* Avellaneous (brown); 255–286–316 $\mu$  in diameter, 10 spores measured; with low, narrow ridges (Fig. 9–10).—The strobili seem to be made up of a few megasporangia at the base and microsporangia above.

*Microspores.* Bittersweet Orange; 24–28–32 $\mu$  in diameter, 20 spores measured; with sparse low, narrow ridges; all spores in tetrads.

*Selaginella martensii* Spring.

*Megaspores.* White; 347–387–418 $\mu$  in diameter, 10 spores measured; with low ridges.—The lower half of the strobilus appears to be megasporangiate and the upper half microsporangiate.

*Microspores.* Flame Scarlet; 21–23–26 $\mu$  in diameter, 11 spores measured; with few, low, broad papillae which occasionally coalesce into ridges; many in tetrads.—The spores were perhaps immature.

*Selaginella estrellensis* Hieron.

*Megaspores.* Pale Ochraceous Buff (very pale orange); 306–377–484 $\mu$  in diameter, 6 spores measured; with very low, narrow ridges, minute papillae on and between the ridges; megasporangia basal.—The larger spores were broken in preparation, so the measurements more strongly reflect the smaller two spores of each sporangium.



*Microspores.* Pale Orange-Yellow; 23–25–29 $\mu$  in diameter, 20 spores measured.—Most of the spores were in tetrads with only slight markings and were probably immature.

*Selaginella mollis* A. Braun.

*Megaspores.* Cream Color; 255–270–301 $\mu$  in diameter, 7 spores measured; with low, narrow ridges (Fig. 15–16).—The strobili are made up largely of megasporangia with a few microsporangia at the top.

*Microspores.* Bittersweet Orange; 21–23–28 $\mu$  in diameter, 20 spores measured; papillae short.

*Selaginella minima* Spring.

*Megaspores.* White; 260–270–275 $\mu$  in diameter, 8 spores measured; with low, narrow ridges.

*Microspores.* None found.

*Selaginella porphyrospora* A. Braun.

*Megaspores.* Bittersweet Orange; 205–255 $\mu$  in diameter, 2 spores measured; with broad muri of medium height (Fig. 6).—Most of the spores were broken in preparation. The megasporangia predominate with the microsporangia in no particular part of the strobilus.

*Microspores.* Capucine Orange; 43–47–55 $\mu$  in diameter, 20 spores measured; walls very thin, decorated with a granular material; mostly broken.

*Selaginella novae-hollandiae* (Sw.) Spring.

*Megaspores.* Off-white; 188–202–218 $\mu$  in diameter, 8 spores measured; strobili with very few, basal megasporangia.

*Microspores.* Bittersweet Orange; 18–19–21 $\mu$  in diameter, 10 spores measured; with long, slender, capitate projections; mostly shed in tetrads.

*Selaginella flagellata* Spring.

*Megaspores.* Cream Color; 214–224–240 $\mu$  in diameter, 6 spores measured; with low, narrow ridges.—The lower half of the strobilus is megasporangiate.

*Microspores.* Mikado Orange; 22–25–26 $\mu$  in diameter, 20 spores measured; with long, slender, capitate papillae (Fig. 38–39).

*Selaginella* unknown species 1.

*Megaspores.* White; 194–235–255 $\mu$  in diameter, 10 spores measured; with low, narrow ridges.

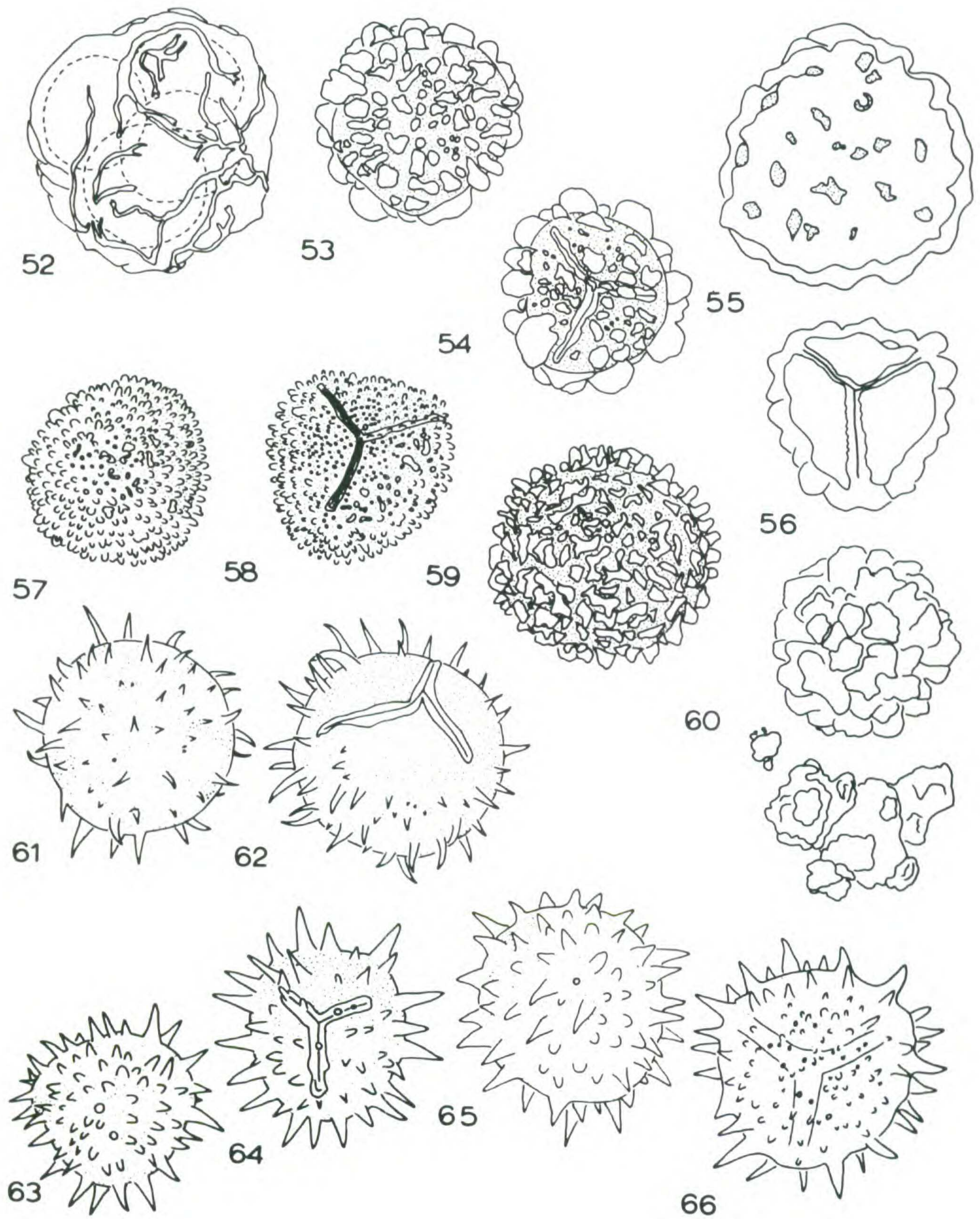
*Microspores.* Capucine Yellow (orange); 22–24–26 $\mu$  in diameter, 20 spores measured; papillae short and broad or elongate and slightly capitate.

*Selaginella* unknown species 2.

*Megaspores.* Cream Color; 255–291–342 $\mu$  in diameter, 10 spores measured; with low, narrow ridges.

*Microspores.* Chrome Orange; 25–29–31 $\mu$  in diameter, 20 spores measured; with long, thin, capitate papillae.







Presumed hybrid.

*Megaspores.* Cream Color; 646–803–1019 $\mu$  in diameter, 4 spores measured; variously marked with irregular ridges; spores very irregular in shape and size; one spore per sporangium; one or two megasporangia at the base of each strobilus (Fig. 25).

*Microspores.* Flame Scarlet; spores mostly abortive; walls marked with heavy, irregular bumps and ridges (Fig. 60).—This collection is presumably a hybrid between *Selaginella pallescens* and some unknown species. The spores are mostly abortive and the plants similar to *S. pallescens*, though they do not fit the characters of that species or any other known to me. Hybridization has been little studied in *Selaginella*, so this collection is specially noteworthy.

#### ARTICULATE SPECIES

*Selaginella exaltata* (Kunze) Spring.

*Megaspores.* Salmon-Orange (pale orange) with off-white ridges; 1,058–1,117–1,176 $\mu$  in diameter, 10 spores measured; with high, narrow muri and irregular thickenings in areoles and on the muri (Fig. 28–29).—There is one basal megasporangium per strobilus.

*Microspores.* Light Buff (sand); 22–25–28 $\mu$  in diameter, 20 spores measured; with many, slender, somewhat capitate projections (Fig. 40–41).

*Selaginella articulata* (Kunze) Spring.

*Megaspores.* Ochraceous-Salmon (beige) with white ridges; 529–568–588 $\mu$  in diameter, 4 spores measured; high, broad ridges (Fig. 30–31).—There is one basal megasporangium per strobilus.

*Microspores.* Light Buff (sand); 22–25–29 $\mu$  in diameter, 20 spores measured; with spines (Fig. 63–64).

*Selaginella arthritica* Alston.

*Megaspores.* Light Buff (sand) with off-white ridges; 206–245–303 $\mu$  in diameter, 7 spores measured; with broad muri of medium height (Fig. 26–27).—There is wide variation in spore size and frequently three small spores and one large spore in each sporangium. There is one basal megasporangium per strobilus.

*Microspores.* Light Buff (sand); 22–31–35 $\mu$  in diameter, 20 spores measured; spines with rather wide, crowded bases.

*Selaginella maginata* (Humb. & Bonpl.) Spring.

*Megaspores.* Light Salmon-Orange; 458 $\mu$  in diameter, one spore measured; with high, very slender muri.—The spore walls are very thin and break easily,



FIGURES 52–66.—Microspores of *Selaginella*. — 52. *S. novoleonensis*, tetrad,  $\times 395$ . — 53–54. *S. schiedeana*,  $\times 580$ .—53. Distal face.—54. Proximal face. — 55–56. *S. schaffneri*,  $\times 580$ .—55. Distal face.—56. Proximal face. — 57–59. *S. delicatissima*,  $\times 580$ .—57, 59. Distal face.—58. Proximal face. — 60. Presumed hybrid,  $\times 580$ . — 61–62. *S. silvestris*,  $\times 580$ .—61. Distal face.—62. Proximal face. — 63–64. *S. articulata*,  $\times 660$ .—63. Distal face.—64. Proximal face. — 65–66. *S. horizontalis*,  $\times 660$ .—65. Distal face.—66. Proximal face.



thus only one measurement was possible. There is one basal megasporangium per strobilus.

*Microspores.* Capucine Buff (beige); 20–26–34 $\mu$  in diameter, 20 spores measured; projections sparse, ranging from long papillae to broad, blunt spines (Fig. 50–51).

*Selaginella sertata* Spring.

*Megaspores.* Cream Color with white ridges; 382–494–526 $\mu$  in diameter, 10 spores measured; with high, narrow muri, aeroles crossed by minor ridges; one basal megasporangium per strobilus (Fig. 21–22).

*Microspores.* Light Ochraceous Buff (beige); 22–25–29 $\mu$  in diameter, 20 spores measured; spines long on the distal face and very short on the proximal face.

*Selaginella silvestris* Aspl.

*Megaspores.* None found.

*Microspores.* Pale Ochraceous Buff (beige); 28–40–47 $\mu$  in diameter, 20 spores measured; spines limited to the distal face and more distantly spaced than in other species of the articulate group; spines variable in size from spore to spore (Fig. 61–62).

*Selaginella galeottii* Spring.

*Megaspores.* Buckthorn Brown with off-white ridges; 382–443–494 $\mu$  in diameter, 8 spores measured; with broad muri of medium height; one basal megasporangium per strobilus.

*Microspores.* Pale Yellow-Orange (beige); 25–31–39 $\mu$  in diameter, 20 spores measured; spines on both faces.

*Selaginella intacta* Baker.

*Megaspores.* Light Buff (sand) with off-white ridges; 347–437–526 $\mu$  in diameter, 10 spores measured; with low, broad muri, minute papillae in the areoles; generally two large and two small spores in each sporangium (Fig. 23–24).—The strobili are wholly microsporangiate, have a basal megasporangium and no other sporangia above, or have a basal megasporangium and a few microsporangia at the top of the strobilus.

*Microspores.* Cinnamon Buff (tan); 22–30–36 $\mu$  in diameter, 20 spores measured; with spines.

*Selaginella horizontalis* (Presl) Spring.

*Megaspores.* Cream Color (off-white); 357–377–437 $\mu$  in diameter, 10 spores measured; narrow muri of medium height; one basal megasporangium with 3 large and 1 small spore per strobilus.

*Microspores.* Pale Ochraceous Buff (beige); 24–28–31 $\mu$  in diameter, 20 spores measured; with spines (Fig. 65–66).

*Selaginella eurynota* A. Braun.

*Megaspores.* Cinnamon (brown), muri almost white; 448–479–510 $\mu$  in diameter, 10 spores measured; with high, narrow muri.—There is one basal mega-



sporangium per strobilus and tendency toward inequality of spore size in any one sporangium.

*Microspores.* Pale Yellow-Orange (beige); 22–29–36 $\mu$  in diameter, 20 spores measured; spines quite crowded.

*Selaginella schizobasis* Baker.

*Megaspores.* Light Pinkish Cinnamon (pale brown) with white ridges; 301–372–523 $\mu$  in diameter, 5 spores measured; with broad muri of medium height; some sporangia with one larger and some with two larger spores.—There is one basal megasporangium per strobilus.

*Microspores.* Pale Orange-Yellow (beige); 18–30–42 $\mu$  in diameter, 20 spores measured; with spines.

*Selaginella kunzeana* A. Braun.

*Megaspores.* White; 382–443–464 $\mu$  in diameter, 10 spores measured; ridges of medium height and width, areoles with many papillae.—There is one basal megasporangium per strobilus.

*Microspores.* Capucine Buff (tan); 26–31–34 $\mu$  in diameter, 20 spores measured; with spines.

KEY TO HETEROPHYLLOUS SELAGINELLAE

- 1. Microspores not spiny, with blunt projections, ridges or no ornamentation; orange in color; megasporangia more than one per strobilus or, if only one, not located at base of strobilus (Non-articulate group) . . . . . 2
- 2. Microspores shed in tetrads encased in a common sculptured wall . . . . .  
*S. lepidophylla*, *S. novoleonensis*
- 2. Microspores generally shed separately, if in tetrads never encased in a common wall . . . . . 3
- 3. Microspores with projections other than elongate ridges . . . . . 4
- 4. Microspores with capitate projections . . . . . 5
- 5. Megaspores averaging 200–290 $\mu$  (188–291 $\mu$ ) in diameter; papillae of microspores usually long and slender . . . . . 6
- 6. Megaspores averaging 200–240 $\mu$  (188–255 $\mu$ ) in diameter, little breakage in preparation . . . . . 7
- 7. Microspores averaging 19 $\mu$  (18–21 $\mu$ ) in diameter, often shed in tetrads; megasporangia very few . . . . . *S. novae-hollandiae*
- 7. Microspores averaging 25–30 $\mu$  (22–31 $\mu$ ) in diameter, shed individually; megasporangia numerous . . . . . 8
- 8. Megasporangia located in the lower half of the strobili; microspores with slender papillae . . . . .  
*Selaginella* unknown sp. 1, *S.* unknown sp. 2, *S. flagellata*
- 8. Megasporangia arranged in two longitudinal rows; microspores with stout papillae often with divided heads. . . . .  
*S. cladorrhizans*
- 6. Megaspores averaging 275 $\mu$  (255–291 $\mu$ ) in diameter, much breakage in preparation . . . . . *S. tarapotensis*
- 5. Megaspores averaging 315–420 $\mu$  (300–448 $\mu$ ) in diameter; papillae of microspores usually short and stout . . . . . 9
- 9. Megaspores averaging 420 $\mu$  (387–448 $\mu$ ) in diameter; microspores averaging 22 $\mu$  (21–24 $\mu$ ) in diameter; megasporangia basal . . . . . *S. pallescens*
- 9. Megaspores averaging 315–350 $\mu$  (300–398 $\mu$ ) in diameter; microspores averaging 30–36 $\mu$  (26–40 $\mu$ ) in diameter; megasporangia not basal . . . . . 10



10. Megasporangia in two longitudinal rows; papillae of microspores with massive, round heads ..... *S. bombycina*
10. Megasporangia in no constant arrangement; papillae of microspore heads not massive ..... 11
11. Papillae of microspores often with split heads. . . *S. pulcherrima*
11. Papillae of microspores all with round heads. . . *S. microdendron*
4. Microspores with non-capitate papillae ..... 12
12. Microspores averaging  $35\text{--}50\mu$  ( $29\text{--}56\mu$ ) in diameter ..... 13
13. Megaspores and microspores with similar papillate markings; megaspores averaging  $475\mu$  ( $443\text{--}496\mu$ ) in diameter. *S. delicatissima*
13. Megaspores with ridges unlike the papillae of the microspores; megaspores averaging not more than  $425\mu$  ( $219\text{--}469\mu$ ) in diameter ..... 14
14. Megaspores averaging  $400\mu$  ( $331\text{--}469\mu$ ) in diameter; usually 3 large and 1 small spore in each megasporangium; microspore papillae irregular in size ..... *S. schiedeana*
14. Megaspores averaging  $225\mu$  ( $219\text{--}240\mu$ ) in diameter; all spores in each megasporangium of equal size; microspore papillae regular in size ..... *S. ovifolia*
12. Microspores averaging  $20\text{--}25\mu$  ( $19\text{--}29\mu$ ) in diameter ..... 15
15. Microsporangia few, scattered in the strobili ..... *S. anceps*, *S. mollis*
15. Microsporangia equal to or exceeding in number the megasporangia which are either basal or in two longitudinal rows .... 16
16. Megasporangia basal; megaspores averaging  $290\text{--}375\mu$  ( $245\text{--}484\mu$ ) in diameter ..... 17
17. Megaspores averaging  $290\mu$  ( $245\text{--}321\mu$ ) in diameter. *S. illecebrosa*
17. Megaspores averaging  $375\mu$  ( $306\text{--}484\mu$ ) in diameter. *S. estrellensis*
16. Megasporangia in two longitudinal rows; megaspores averaging  $225\text{--}235\mu$  ( $204\text{--}296\mu$ ) in diameter ..... *S. haematodes*, *S. umbrosa*
3. Microspores with elongate ridges, heavy ridge-like papillae, or with no markings at all ..... 18
18. Microspores with no markings or with very thin walls covered with a granular material ..... 19
19. Microspores with no markings ..... *S. revoluta*
19. Microspores with thin walls covered with a granular material ... *S. porphyrospora*
18. Microspores with ridges ..... 20
20. Microspores with ridges covering most of the surface, ridges very low, up to  $8\mu$  wide; microspores averaging  $56\mu$  ( $47\text{--}63\mu$ ) in diameter ..... *S. schaffneri*
20. Microspores with ridges not covering most of surface, ridges with distinguishable height, not more than  $5\mu$  wide; microspores averaging  $23\text{--}28\mu$  ( $20\text{--}36\mu$ ) in diameter ..... 21
21. Microspores with heavy, ridge-like, amorphous papillae ..... 22
22. Megasporangia very few, often only one per strobilus; papillae of microspores ridge-like only at the equator. .... *S. reflexa*
22. Megasporangia numerous; papillae of microspores ridge-like on the distal face as well as at equator ..... 23
23. Megasporangia basal ..... *S. stenophylla*
23. Megasporangia in two longitudinal rows ..... *S. lychnuchus*
21. Microspores with thin precise ridges or very faint ones, never massive ..... 24
24. Microspores with faint amorphous ridges ..... 25
25. Megaspores with papillae on the proximal face . . *S. oaxacana*
25. Megaspores without papillae on the proximal face. *S. martensii*
24. Microspores with precisely marked ridges up to  $3\mu$  wide usually with distinguishable height, especially at the equa-



- tor of the spore ..... 26
26. Microspore ridges never extended to form blunt spine-like projections; microspores often shed in tetrads. . . . . *S. idiospora*
26. Microspore ridges often elongated into blunt spine-like projections; microspores not shed in tetrads ..... 27
27. Megaspores averaging  $275\mu$  ( $240-316\mu$ ) in diameter; megasporangia in two longitudinal rows ...  
*S. hoffmannii*
27. Megaspores averaging  $375\mu$  ( $316-458\mu$ ) in diameter; megasporangia basal .....  
*S. guatemalensis, S. huehuetenangensis*
1. Microspores with sharp-pointed spines (except *S. exaltata* and *S. marginata*); microspores tan (except pale orange-tan in *S. marginata*); megasporangium one, basal; strobilus usually conspicuously swollen at base; megaspores with high, definite muri (Articulate group) ..... 28
28. Microspores lacking sharp projections ..... 29
29. Microspores with slender blunt projections; megaspores averaging  $1,115\mu$  ( $1,058-1,176\mu$ ) in diameter ..... *S. exaltata*
29. Microspores with wide flattened projections; megaspores averaging  $450\mu$  ( $-458\mu$ ) in diameter ..... *S. marginata*
28. Microspores with sharp-pointed spines ..... 30
30. Microspores averaging  $40\mu$  ( $28-47\mu$ ) in diameter; microspore spines few ..... *S. silvestris*
30. Microspores averaging  $25-31\mu$  ( $18-42\mu$ ) in diameter; spines numerous .... 31
31. Three large and 1 small or 2 large and 2 small spores in each megasporangium ..... 32
32. Megaspores averaging  $250\mu$  ( $206-303\mu$ ) in diameter ..... *S. arthritica*
32. Megaspores averaging  $375-480\mu$  ( $301-526\mu$ ) in diameter ..... 33
33. Megaspores averaging  $370-380\mu$  ( $301-523\mu$ ) in diameter ..... 34
34. Megaspores pale brown with white ridges; megaspore muri up to  $15\mu$  wide ..... *S. schizobasis*
34. Megaspores off-white; megaspore muri up to  $5\mu$  wide ....  
*S. horizontalis*
33. Megaspores averaging  $435-480\mu$  ( $347-510\mu$ ) in diameter ..... 35
35. Strobili often varying from the one basal megasporangium pattern ..... *S. intacta*
35. Strobili always with one basal megasporangium ..... *S. eurynota*
31. All spores in each megasporangium of equal size ..... 36
36. Megaspores averaging  $570\mu$  ( $529-588\mu$ ) in diameter ..... *S. articulata*
36. Megaspores averaging  $440-500\mu$  ( $382-526\mu$ ) in diameter ..... 37
37. Megaspores with muri up to  $25\mu$  wide; megaspores brown with white muri ..... *S. galeottii*
37. Megaspores with muri  $10-15\mu$  wide; megaspores white or cream color with off-white muri ..... 38
38. Megaspores cream with white muri; megaspore areoles crossed by minor ridges ..... *S. sertata*
38. Megaspores white; megaspore areoles with many minute papillae ..... *S. kunzeana*

## OBSERVATIONS

*Spore Color.* The muri and ridges of megaspores are often a different color than the spore wall, so it is often difficult to judge the color of the spores. There also seems to be a tendency toward loss of color or change in color with age. One specimen was annotated as having yellow spores, but only brown ones could be found. The color of the megaspores is so variable as to be of little use in segregating groups. None of the species groups in Alston's key (1955) is characterized by any one color.



Microspore color, on the other hand, shows a nearly perfect correlation with stem articulation. The microspores of the non-articulate species are all some shade of orange; those of the articulate species are tan.

*Spore Size.* Megaspore size is extremely diverse, ranging from  $224\mu$  in *S. flagellata* to 1.2 mm in *S. exaltata*. However, size gives little indication of relationship. With the exception of *S. arthritica*, megaspores of the articulate species are large, but several non-articulate species also have large spores.

Within a single megasporangium the spore size may vary. In some species there are regularly one large and three small spores, and in other species regularly two large and two small spores. Certain species may vary as to the spore size relationship in different sporangia. This variability is found in both articulate and non-articulate species. A more detailed investigation is needed both on megaspore ontogeny and on viability of the different-sized spores. There may be a trend toward a single functional megaspore.

Microspore sizes are mostly between 20 and  $30\mu$ , although a few species have much larger spores. *Selaginella schaffneri*, for example, has microspores  $56\mu$  in diameter. Microspore size, however, is apparently not correlated with taxonomic groupings, and the larger microspores may be a result of polyploidy.

*Spore Wall Ornamentation.* The wall ornamentation of the megaspores is not easily characterized; however, some types can be recognized. The spores of the articulate species generally have higher muri than those of the non-articulate species. Within the articulate species the spores may be further divided on the basis of height and width of the muri. High, narrow muri are found in *S. exaltata* (Fig. 28–29) and *S. sertata* (Fig. 21–22). Low, broad muri occur on the spores of *S. articulata* (Fig. 30–31).

The megaspores of the non-articulate species generally have low ridges (Fig. 11, 17). Correlated with the lower ridges is a lesser degree of ornamentation on the proximal face. There are, however, a few species of the non-articulate group, such as *S. mollis* (Fig. 15–16), which have spores with narrow muri similar to those of the articulate species. Most commonly the megaspores of the non-articulate group have ridges which vary from low, broad ones which are nearly free of anastomoses in *S. tarapotensis* (Fig. 17–18) to very low ones which run together freely but still leave many free ends, as in *S. pallescens* (Fig. 7–8).

These spores have different markings on their proximal faces ranging from pointed peaks on the low ridges in *S. guatemalensis* (Fig. 2) to low papillae in *S. oaxacana* (Fig. 12). This papillosity is carried to the extreme in *S. delicatissima* (Fig. 19–20) in which papillae are the only markings on all faces. This species is the only one studied in which megaspores and microspores look alike.

The ornamentation of the microspores also reflects the distinctness of the articulate group and the non-articulate group. The articulate species generally have sharp-pointed spines (Fig. 61–66), which no members of the non-articulate group have. The only two articulate species that lack spines are *S. marginata* (Fig. 50–51), which has long, broad projections, and *S. exaltata* (Fig. 40–41), which has long, somewhat capitate papillae closely resembling those found in many non-articulate species (Fig. 38–39).



Papillae seem to be the basic type of ornamentation on the microspores of the non-articulate species; there are several variations of this general shape. *Selaginella umbrosa* (Fig. 32–33) has representative papillose microspores. *Selaginella delicatissima* (Fig. 57–58) has very small papillae which cover all faces, but the papillae may coalesce to form short ridges (Fig. 59). The papillae are short and massive in *S. ovifolia* (Fig. 46–47) and *S. reflexa* (Fig. 48–49).

Capitate papillae reach two extremes. *Selaginella tarapotensis* (Fig. 36–37), for example, has short, stout projections. *Selaginella flagellata* (Fig. 38–39), on the other hand, has long, narrow, capitate projections.

In some species microspore ornamentation is in the form of ridges. Ridges are very short and indistinct in *S. oaxacana*, whereas in other species such as *S. idiospora* (Fig. 42–43), the ridges are definite but not anastomosing. The ridges are long and anastomosing, ending in spine-like projections in *S. guatemalensis* (Fig. 44–45) and *S. huehuetenangensis*. The wall of *S. schaffneri* (Fig. 55–56) is distinctive in being extremely thick with scattered depressions. This pattern may possibly be formed from fusion of broad papillae or ridges.

*Selaginella revoluta* (Fig. 34–35) is the only species with microspores which do not have any ornamentation at all. The spores are assumed to be mature since they were all free of tetrads.

Perhaps the most distinctive microspore specialization is found in those species characterized by the plants curling into a ball in dry seasons. These species represented by *S. novoleonensis* (Fig. 52) and *S. lepidophylla*, shed their microspores in tetrads. Apparently the heavy outer wall is common to the entire tetrad and is ornamented by several ridges. Furthermore, there seems to be a tendency among many of the other non-articulate species to shed at least some of their microspores in tetrads.

*Sporangial Arrangement.* Sporangial arrangement patterns in 42 species were apparent. Once again the articulate species display a common pattern — a single basal megasporangium with many microsporangia above it. *Selaginella intacta* of the articulate group has some strobili with two megasporangia at the base.

Among the non-articulate species only *S. schaffneri* and *S. schiedeana* have a single basal megasporangium. Other patterns found include the lower half of the strobilus being megasporangiate and the upper half microsporangiate (*S. delicatissima*), two rows of megasporangia and two of microsporangia (*S. bombycina*), a very few megasporangia scattered in the strobilus (*S. lepidophylla*), and a very few microsporangia in the strobilus (*S. anceps*) with *S. revoluta* being the extreme with one microsporangium at the tip of the strobilus.

#### CONCLUSIONS

The spores of *Selaginella* are of considerable taxonomic value. Alston (1955) used them in his key to separate some species, but he did not use them in separating larger groups of species. The present study shows that certain spore characters can be useful in defining these groups.

The most obvious separation based on spore characters is between the articulate and non-articulate species. Four spore characters — microspore color and



ornamentation, megaspore ornamentation and size — plus sporangial arrangement indicate the distinctness of the two groups. The spores of the articulate species are not as diverse as those of the non-articulate group; therefore, the latter group can more easily be further divided on the basis of spore characters.

Within the non-articulate group the *S. lepidophylla* group seems to be distinct based on spore characters as well as other morphological features. The microspores shed in tetrads encased in heavy common walls in this group is unique among the species studied.

Other groupings in Alston's key (1955) were not upheld as well by spore characters. However, some species, such as *S. guatemalensis* and *S. huehuetenangoensis*, which occur together in the key, have similar spores. More detailed studies may help define more groups based on the spore characters within the heterophyllous *Selaginellae*.

Several additional problems which could be investigated with profit presented themselves in the course of this work. Studies of sporangial arrangement, spore ontogeny, hybridization and polyploidy, and spore ornamentation on a worldwide basis would prove to be of developmental, morphological, and taxonomic interest.

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